

POPULATION TRENDS OF TUNDRA-NESTING BIRDS AT CAPE CHURCHILL, MANITOBA, IN RELATION TO INCREASING GOOSE POPULATIONS

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Abstract. To assess potential changes in tundra-nesting bird populations relative to increased herbivory by growing Lesser Snow Goose (*Chen caerulescens caerulescens*) and Ross's Goose (*C. rossii*) populations, we estimated avian population densities in coastal tundra near Cape Churchill, Manitoba, Canada in June 1984, 1999, and 2000. We also compared bird abundance in altered and intact freshwater sedge (*Carex* spp.) meadows to assess bird response at a smaller spatial scale, the habitat patch. At the landscape scale, Herring Gull (*Larus argentatus*) densities were significantly greater in both 1999 and 2000 than 1984, and Semipalmated Sandpiper (*Calidris pusilla*) and Savannah Sparrow (*Passerculus sandwichensis*) densities were greater in 2000 than 1984. As a group, tundra-nesting passerine densities were significantly greater in 1999 than 1984. Dunlin (*Calidris alpina*) densities were significantly lower in 1999 than 1984, and many larger, ground-nesting birds declined in abundance and occurrence along transects in later years. At the smaller spatial scale, passerines and shorebirds were less abundant in altered than intact freshwater sedge meadows. Our results indicate that most abundant breeding birds on the study area did not exhibit lower densities in later years despite increased effects of goose herbivory on vegetation. At the habitat patch scale, the same groups of species had lower abundances in altered versus largely intact habitats. Although goose herbivory can alter tundra vegetation and lead to lower abundance of several bird species, habitat alteration may have to be widespread and severe to elicit population declines over a large area.

Key words: Churchill, line transects, population, Snow Goose, trends, tundra-nesting birds.

Tendencias Poblacionales de Aves que Anidan en la Tundra en Cabo Churchill, Manitoba, en Relación con el Incremento de las Poblaciones de Gansos

Resumen. Para evaluar los cambios potenciales en las poblaciones de aves que anidan en la tundra relacionada con un aumento en la herbivoría causado por el crecimiento de las poblaciones de *Chen caerulescens caerulescens* y *C. rossii*, estimamos las densidades poblacionales de aves en la tundra costera cerca de Cabo Churchill, Manitoba, en junio de 1984, 1999 y 2000. También comparamos la abundancia de aves en prados dulceacuícolas de *Carex* spp. alterados e intactos para evaluar la respuesta de las aves a la escala espacial más pequeña, el parche de hábitat. A la escala de paisaje, las densidades de *Larus argentatus* fueron significativamente mayores en 1999 y 2000 que en 1984, y las densidades de *Calidris pusilla* y *Passerculus sandwichensis* fueron mayores en 2000 que en 1984. Como grupo, las densidades de paserinos que anidan en la tundra fueron significativamente mayores en 1999 que en 1984. Las densidades de *Calidris alpina* fueron significativamente menores en 1999 que en 1984, y la abundancia y presencia a lo largo de transectas de muchas aves más grandes que anidan sobre el suelo disminuyó en los años siguientes. A la escala espacial más pequeña, los paserinos y las aves playeras fueron menos abundantes en prados dulceacuícolas de *Carex* intactos. Nuestros resultados indican que la mayoría de las aves abundantes que anidan en el área de estudio no mostraron menores densidades en los años siguientes, a pesar del incremento de los efectos de la herbivoría de los gansos sobre la vegetación. A la escala de parche de hábitat, el mismo grupo de especies presentó abundancias menores en los ambientes alterados que en los que estaban mayormente intactos. Aunque la herbivoría de los gansos puede alterar la vegetación de la tundra y provocar una menor abundancia de varias especies de aves, la alteración del hábitat podría necesitar ser ampliamente difundida y severa para generar disminuciones poblacionales a lo largo de una gran área.

INTRODUCTION

Over the past 30 years, populations of midcontinent Lesser Snow Geese (*Chen caerulescens caerulescens*) and Ross's Geese (*C. rossii*) have increased significantly in North America (Ankney 1996, Batt 1997). Lesser Snow Geese are

philopatric (Cooke et al. 1975, Cooke and Abraham 1980), resulting in increased densities of geese at tundra breeding-colony sites over time. High goose population densities have led to increased herbivory and alteration of vegetation at traditional nesting and staging areas (Kerbes et al. 1990, Abraham and Jefferies 1997, Jano et al. 1998). Lesser Snow Geese "grub"

Manuscript received 27 July 2007; accepted 2 May 2008.

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(i.e., dig up roots and rhizomes of tundra vegetation) and pull shoots, which disrupts the wetland substrate (Abraham and Jefferies 1997). Heavy and continued goose foraging leads to the creation of nonvegetated patches across the landscape. Consequently, there is increased erosion, sedimentation, and development of hypersaline conditions, dramatically altering resulting habitat patches, with long projected times for recovery (Kerbes et al. 1990, Iacobelli and Jefferies 1991, Srivastava and Jefferies 1996, Jefferies et al. 2006). As habitat conditions are altered within breeding colonies, Lesser Snow Geese have occupied less altered habitats, extending the effects of goose herbivory. In addition, foraging by migrating and staging geese affects areas well away from breeding colonies (Jano et al. 1998).

The extent of current habitat alteration varies across the landscape. Salt marsh plant communities are preferred by Lesser Snow Geese, and as a result, on the western shore of Hudson Bay, a large portion of salt marsh vegetation has been removed by geese and replaced by exposed sediment (Abraham and Jefferies 1997, Jefferies et al. 2003, 2006). As salt marsh habitat has deteriorated, Lesser Snow Geese have started foraging in the extensive, inland freshwater sedge (*Carex* spp.) meadow plant communities, which currently are not as affected by goose herbivory. However, with increasing goose numbers and expansion of nesting colonies, freshwater sedge meadow habitats are experiencing increased foraging pressure and resulting habitat alteration from goose herbivory.

Relatively little information is available on the effects of this habitat alteration on other bird species, although ecosystem-level changes are occurring over a wide area (Jefferies et al. 2006). This is partially due to the paucity of data on basic breeding population trends for Nearctic tundra-nesting birds (Gratto-Trevor et al. 1998). However, based on annual bird sightings at La Pérouse Bay, Manitoba, Canada, Abraham and Jefferies (1997) concluded that up to 30 species of birds have shown significant declines in abundance within a Snow Goose breeding colony concurrent with habitat alteration caused by nesting and foraging Snow Geese. In addition, apparent declines in nest densities of Red-necked Phalaropes (*Phalaropus lobatus*), Semipalmated Sandpipers (*Calidris pusilla*), and Savannah Sparrows (*Passerculus sandwichensis*) occurred between 1984 and the 1990s (Abraham and Jefferies 1997, Rockwell et al. 2003), and Jehl (2007) recently reported on declines in breeding Semipalmated Sandpipers near Churchill, Manitoba, Canada.

Most existing indications of tundra bird population declines are from areas in close proximity to Snow Goose breeding colonies, where habitat alteration is severe and widespread. However, there are varying levels of habitat alteration across the larger tundra landscape. With continuing population growth, the extent of area where vegetation changes have occurred as a result of goose foraging has expanded, resulting in low to

moderate levels of habitat alteration in small patches within a matrix of less affected habitat. Bird populations inhabiting areas of low to moderate habitat alteration may show different population trends than birds occupying severely affected areas. Thus, it is important to understand how bird populations respond to slight to moderate habitat alteration in addition to severe habitat alteration, because lower levels of habitat alteration are more typical throughout the tundra landscape.

Herein, we report on population densities of tundra-nesting birds in the same landscape as a historical Lesser Snow Goose colony in Manitoba, Canada, where habitat alteration has occurred to a lesser degree than within the colony. Our objectives were to: (1) determine if tundra-nesting bird densities were significantly different at a landscape scale between 1984 and 1999–2000 with increasing goose-mediated habitat alteration, and (2) assess bird abundance at the habitat-patch scale in altered versus largely intact freshwater sedge meadow habitats.

METHODS

STUDY AREA

Our Cape Churchill study area is located 60 km east of Churchill, Manitoba and 15 km southeast of the La Pérouse Bay Snow Goose colony core in Wapusk National Park (Fig. 1). Base camp (Nestor One) is located approximately 2 km west from the Hudson Bay coast, where Canada Goose (*Branta canadensis*) productivity has been studied since 1968 (Walter 1999). The study area encompasses approximately 48 km², is characterized as a tundra biome, and lies within the Hudson Bay Lowlands physiographic region (Wellein and Lumdsen 1964). The area is composed of a series of coastal salt marshes and freshwater sedge

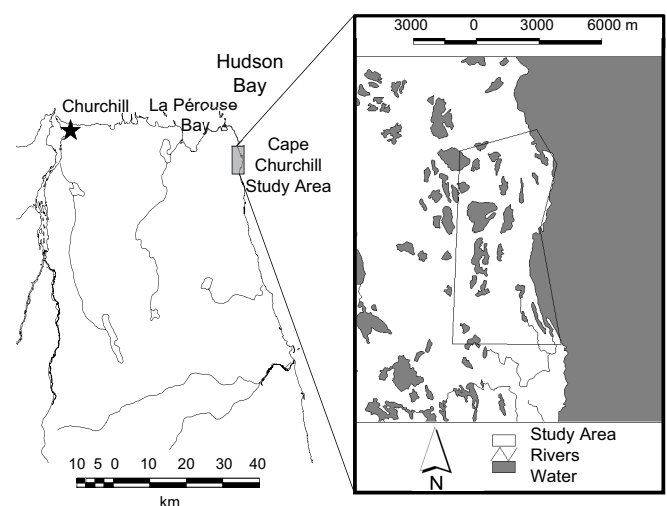


FIGURE 1. Location of the Cape Churchill study area in northern Manitoba, Canada where bird surveys were conducted in 1984, 1999, and 2000 to assess breeding bird populations in relation to increasing goose abundance.

meadows interspersed with relict beach ridges. The surrounding landscape consists of large, permanent, freshwater lakes, ephemeral freshwater pools, and freshwater sedge meadows. Existing landscape features, such as permafrost, minimal relief, and permanent water bodies, are a result of Pleistocene glaciation. Isostatic uplift, or the uplifting of land after the retreat of glaciers, occurs at a rate of 1–1.5 m century⁻¹ (Hunter 1970).

Beach ridges on the study site are characterized by higher elevation than surrounding freshwater sedge meadow communities and dominance of lyme grass (*Elymus arenarius*) and white mountain avens (*Dryas integrifolia*). Lowland wet areas are dominated by sedges (primarily *Carex aquatilis*). Small patches of willows (*Salix* spp.), white spruce (*Picea glauca*), and larch (*Larix laricina*) occur on dry, inland areas. Coastal areas are dominated by lyme grass and sedges among rocky and gravelly substrates. Most vegetation communities at Cape Churchill are arranged parallel to the coast. For more extensive descriptions of vegetation at the Nestor One study area, refer to Didiuk and Rusch (1979), Johnson (1987), and Brook (2001).

The study area has patches of altered habitat, consistent with those resulting from goose foraging activities. These areas are characterized by loss of vegetation or presence of a moss carpet (Jefferies 1988). Coastal salt marshes are completely altered, with only muddy substrates and underlying rocks remaining (Jefferies et al. 2006). Sections of freshwater sedge meadows exhibit varying habitat alteration, from severe to none.

Spring phenology on our study area is highly variable, and environmental conditions during the breeding season may influence arrival and reproduction of migratory birds (Skinner et al. 1998). To account for the potential influence of relative spring conditions on breeding birds in our study, we compared average temperatures at Churchill, Manitoba in late spring and early

summer (April through June) in 1984, 1999, and 2000 to average temperatures from 1943–2000 (Environment Canada 2008).

SURVEY METHODS

Throughout our Cape Churchill study site (Fig. 1), in 1984, we established and surveyed 30 line transects, ranging from 90 to 1870 m in length, based on the methods outlined by Burnham et al. (1980). We surveyed each transect once each year in 1984, 1999, and 2000 between mid-June and early July and between the hours of 12:00 and 20:00 CDT. We conducted surveys during the courtship and early nesting periods of breeding birds on the study area and adjusted survey timing based on observed spring phenology and bird behavior. We surveyed transects on days with winds <25 km hr⁻¹, minimal to no fog or precipitation, and clear to moderately cloudy skies, and recorded any bird visible or audible from a transect line. For each detection, we recorded sex of the bird, compass bearing from the transect line to the bird when first detected, estimated distance from observer to the location of the detected bird, habitat type, and behavior, when possible. In 1984, we estimated distances visually, and these distances were confirmed by a second observer, who periodically checked distances by pacing. In 1999 and 2000, we surveyed transects using the methods used in 1984, but estimated distances using a parallax-type range finder.

Density estimation ($n \geq 30$). We converted sightings from surveys to perpendicular distances from transects to bird locations and entered them into program DISTANCE (Thomas et al. 1998) to estimate density for bird species or guilds with $n \geq 30$ sightings in 1984, 1999, and 2000 (Buckland et al. 1993). We compiled guilds for shorebirds that nest in freshwater sedge meadows, passerines that nest in or are dependent upon willow patches for nesting, and freshwater sedge meadow–nesting passerines (Table 1). To avoid computation

TABLE 1. Nesting guilds of birds observed in surveys at Cape Churchill, Manitoba, Canada in 1984, 1999, or 2000 and used to evaluate changes in breeding bird populations in relation to goose abundance.

Guild	English name	Latin name
Shorebirds	Semipalmated Plover	<i>Charadrius semipalmatus</i>
	Hudsonian Godwit	<i>Limosa haemastica</i>
	Semipalmated Sandpiper	<i>Calidris pusilla</i>
	Least Sandpiper	<i>Calidris minutilla</i>
	Pectoral Sandpiper	<i>Calidris melanotos</i>
	Dunlin	<i>Calidris alpina</i>
	Silt Sandpiper	<i>Calidris himantopus</i>
	Red-necked Phalarope	<i>Phalaropus lobatus</i>
Tundra-nesting passerines	Horned Lark	<i>Eremophila alpestris</i>
	Savannah Sparrow	<i>Passerculus sandwichensis</i>
	Lapland Longspur	<i>Calcarius lapponicus</i>
	Snow Bunting	<i>Plectrophenax nivalis</i>
Willow-nesting passerines	Yellow Warbler	<i>Dendroica petechia</i>
	American Tree Sparrow	<i>Spizella arborea</i>
	White-crowned Sparrow	<i>Zonotrichia leucophrys</i>
	Common Redpoll	<i>Carduelis flammea</i>
	Hoary Redpoll	<i>Carduelis hornemanni</i>

complications resulting from few observations far from transect lines, we truncated observations at 200 m (perpendicular distance) from transect lines in analyses (Buckland et al. 1993). For each species or guild in each year, we fit uniform-cosine, half-normal-cosine, and hazard-polynomial detection functions to the detection data and used Akaike's information criterion (AIC) to distinguish which model was best supported by the detection data (Akaike 1985, Buckland et al. 1993).

In several instances, detection function models selected based on AIC were not the same for all three years for a particular species or guild. To have consistent detection functions among years (Buckland et al. 1993), we chose one common detection function for a species or guild for all years, based on which detection function model was best supported in most years and data from all years combined. As a result, for some species or guild groups, we used a detection function model that did not exhibit the lowest AIC value for a particular year. In these instances, we evaluated detection function model fit using a chi-square goodness-of-fit test. This statistic also assesses detection function model fit, but it is less powerful than AIC (Buckland et al. 1993).

Bird abundance estimation ($n < 30$). Most species detected on surveys did not have large enough sample sizes ($n < 30$) during at least one of the three years to reliably estimate density based on distance sampling. For each of these species, we tallied the total number of individuals seen within 200 m (perpendicular distance) of transects on surveys and divided this number by the total distance traversed on surveys, to estimate encounter rate across transects. For Lesser Snow Geese, we counted any goose detected within 400 m of transects because Snow Geese tended to be approachable only within 300–400 m. We made direct comparisons among years with these data and noted large changes in encounter rates (at least 2.5 times differences among years). We included only species for which we detected ≥ 30 individuals in ≥ 1 year in this analysis.

FRESHWATER SEDGE MEADOW HABITAT COMPARISON

Many transects, originally established in 1984, did not traverse substantial areas of highly altered vegetation that we observed in other portions of the study area in 1999 and 2000. Therefore, to evaluate how bird abundance is affected by habitat alteration, we established three new transects in freshwater sedge meadow habitats with evidence of vegetation alteration resulting from goose foraging, identified based on lack of vegetation or occurrence of extensive moss carpets (Jefferies 1988, Kerbes et al. 1990, Abraham and Jefferies 1997). Twice during mid- to late June 2000, we conducted line transect surveys in habitat patches of largely intact (four original transects) and altered (newly established transects) freshwater sedge meadows between the

hours of 09:00 and 15:00. Survey methods were the same as described for transects conducted in 1999 and 2000. To minimize the influence of distance on detection probability, we counted only birds detected at a perpendicular distance of ≤ 100 m from transects and tallied the total number of birds detected per habitat type (altered vs. largely intact) for species and guilds. We divided the number of detections by the total distance traversed on survey routes and compared this measure of abundance between the two transect classes.

To evaluate vegetation differences between altered and intact habitats, we conducted vegetation measurements along all transects and assessed characteristics thought to be related to habitat alteration resulting from goose herbivory (Kerbes et al. 1990, Jefferies et al. 2006). As outlined by Kerbes et al. (1990), we used a $1 \text{ m} \times 1 \text{ m}$ wooden frame with 25 evenly spaced grid intersections. We began vegetation measurements 25 m from the transect start location at a perpendicular distance of 50 m from each transect line. We then placed the grid on the ground and tallied the types of vegetation or ground cover that grid intersections touched. Vegetation and ground cover types consisted of bare ground, moss, sedge, woody plants, other plants, ephemeral water, permanent water, and other. In addition, we counted the numbers of goose droppings, willow stems, and grubbed turf pieces throughout the grid. After collection of data at a site, we returned to the transect and walked another 50 m and then walked 50 m perpendicular to the transect at this location to the next vegetation measurement location. We alternated taking vegetation measurements to the left and right sides of transects.

STATISTICAL ANALYSES

For line transect density estimation, we estimated density and standard error for each year for species and guilds with sample sizes ≥ 30 . We then constructed 90% and 95% confidence intervals for each estimate and compared point estimates among years based on confidence intervals. We concluded that significant differences were evident if there was no overlap between 90% or 95% confidence intervals (Table 2).

For species with $n < 30$, we determined how many transects had suitable habitat in which a particular species would be expected to occur. We determined expected habitat for a species using knowledge from previous experience as to which vegetation communities were used by nesting or foraging birds (JES and DEA, unpubl. data) and published information about breeding habitat use. Then, for each year, we tallied the proportion of transects with suitable habitat on which we detected each species. We then compared these proportions using a chi-square test, to evaluate if the proportion of transects where birds were detected was related to habitat condition or changed through time. We used a one-tailed chi-square test because survey data indicated that all species (except Snow Geese) with $n < 30$ had declined over

TABLE 2. Density estimates in number of birds km⁻² for species with ≥30 individuals detected each year (1984, 1999, and 2000) at Cape Churchill, Manitoba, Canada, based on line transect analysis.

Species	Detection function	1984	1999	2000	Significance ^a
		Mean ± SE	Mean ± SE	Mean ± SE	
Semipalmated Sandpiper	Hazard-polynomial	14.9 ± 3.5	60.5 ± 28.2	47.7 ± 12.9	**between 1984 and 2000
Dunlin	Uniform-cosine	23.0 ± 3.3	11.8 ± 2.4	22.9 ± 4.4	*between 1984 and 1999
Herring Gull	Uniform-cosine	5.3 ± 0.6	21.2 ± 11.9	18.8 ± 5.1	**
Horned Lark	Hazard-polynomial	24.9 ± 5.6	52.6 ± 15.9	49.3 ± 12.8	
Savannah Sparrow	Half-normal-cosine	32.7 ± 7.0	34.6 ± 5.2	62.1 ± 9.5	*between 1984 and 2000 *between 1999 and 2000
Lapland Longspur	Half-normal-cosine	50.4 ± 7.1	77.3 ± 9.9	47.8 ± 6.5	*between 1999 and 2000
Shorebird guild	Half-normal-cosine	48.1 ± 8.3	75.2 ± 19.7	63.5 ± 11.9	
Tundra-nesting passerines	Hazard-polynomial	74.3 ± 6.8	165.4 ± 31.7	112.9 ± 20.9	**between 1984 and 1999
Willow-nesting passerines	Hazard-polynomial	14.8 ± 6.5	14.7 ± 8.5	43.7 ± 43.8	

^aSignificance was measured via confidence intervals: *indicates 90% confidence intervals; **indicates 95% confidence intervals.

time. Additionally, for each species and guild, we computed the number of birds observed m⁻¹ for each transect on which that species or guild was detected. We used one-way analysis of variance (ANOVA) with $\alpha = 0.05$ to determine whether encounter rates on transects differed among years.

For comparison of bird abundance between altered and intact freshwater sedge meadows, variability in abundance values could result from three sources: variability in individual transects due to varying vegetation types and composition, differences in habitat quality (altered vs. intact), and differences due to the timing of surveys (i.e., ordinal date). We were unable to evaluate potential variation from individual transects because we did not conduct multiple surveys along each transect. To determine if one or both of the latter factors explained a significant proportion of total variation in the survey data, we used a general linear model (GLM; Cook and Weisberg 1999). This model was:

$$\text{Variation in abundance} = \text{variation from habitat quality} \\ + \text{variation from survey times} + \text{error.}$$

We considered factors in the GLM that were significant at $P < 0.05$ to be associated with significant changes in bird abundance.

For comparison of vegetation communities and bird abundances on transects in altered and intact freshwater sedge meadows, we used two-sample, two-tailed *t*-tests, with $\alpha = 0.05$. For each transect, we computed estimates of the mean percent cover of sedge, woody plants, bare ground, moss, altered habitat (bare ground and moss), and non-moss vegetation (sedge, woody, and leafy vegetation). We estimated percent cover as the proportion of intersection points that intercepted a vegetation or ground cover type compared to all non-water points. We averaged all transect cover estimates to get an average cover estimate for the entire transect. Reported values are means ± SE, and significance levels are $P < 0.05$ unless otherwise specified.

RESULTS

Both 1984 and 1999 were relatively warm springs (91st and 100th percentile, respectively, for the period from April through June), and 2000 was cooler than average (25th percentile), based on spring temperatures at Churchill, Manitoba from 1943 to 2000. In both 1984 (75th percentile) and 1999 (98th percentile), average June temperature was warmer than average, and in 2000 (12th percentile) average June temperature was cooler than average.

DENSITY AND ABUNDANCE COMPARISONS

SPECIES OR GUILDS WITH $n > 30$

In 1984, 1999, and 2000, we detected totals of 37, 36, and 34 species on transects, respectively, with ≥30 detections of Dunlins (*Calidris alpina*), Semipalmated Sandpipers, Herring Gulls (*Larus argentatus*), Horned Larks (*Eremophila alpestris*), Savannah Sparrows, and Lapland Longspurs (*Calcarius lapponicus*) in all three years. For Dunlins, sedge meadow-nesting shorebirds, estimated density was lower in 1999 than 1984, but estimated densities in 1984 and 2000 were similar (Table 2). Herring Gulls, habitat generalists, had significantly greater densities in 1999 and 2000 than 1984. There was substantial intra- and interannual variation in abundances of passerine species. As a group, tundra-nesting passerines exhibited significantly greater densities in 1999 than 1984, although there were no significant differences in densities between years for the two abundant species within this guild (Table 2). Estimated density of Semipalmated Sandpiper, a sedge meadow-nesting shorebird, was significantly greater in 2000 than 1984. Densities of the freshwater sedge meadow-nesting shorebird guild did not change significantly from 1984 to 1999 or 2000, despite increases in point estimates of density over time. For the willow-nesting bird guild, we observed no significant changes in density despite a high point estimate in 2000 (Table 2).

SPECIES OR GUILDS WITH $n < 30$

For species with $n < 30$, six (Pacific Loons [*Gavia pacifica*], Long-tailed Ducks [*Clangula hyemalis*], Willow Ptarmigan [*Lagopus lagopus*], Pectoral Sandpipers [*Calidris melanotos*], Red-necked Phalaropes, and Arctic Terns [*Sterna paradisaea*]) were considerably less abundant in 1999 or 2000 than 1984 based on count data. Lesser Snow Geese were more abundant in later years; based on encounter rate data, we observed at least 27 times more Snow Geese on transects in 1999–2000 than in 1984. For species that exhibited decreases in abundance, some of the contrasts were stark. Most notable were the lack of sightings of Pectoral Sandpipers in 1999 and 2000, and of Willow Ptarmigan in 2000. We observed significant reductions in the number of transects on which we detected birds between 1984 and 1999–2000 for Arctic Terns ($\chi^2_1 = 9.2$, $P < 0.003$), Pectoral Sandpipers ($\chi^2_1 = 12.9$, $P < 0.001$), and Willow Ptarmigan ($\chi^2_1 = 4.6$, $P = 0.03$). Arctic Terns had higher encounter rates along transects in 1984 than in 1999 ($F_{2,17} = 2.0$, $P = 0.03$) and 2000 ($F_{2,17} = 1.8$, $P = 0.04$), and Willow Ptarmigan had higher encounter rates on transects in 1984 than in 1999 ($F_{2,10} = 2.4$, $P = 0.02$) and 2000 (we observed no Willow Ptarmigan along transects in 2000).

FRESHWATER SEDGE MEADOW COMPARISONS

Habitat variables. Altered and intact freshwater sedge meadows differed in most of the vegetation characteristics (Table 3) we measured. Transects traversing altered habitats had higher proportions of bare ground, moss, and combined moss and bare ground cover compared to transects across largely intact sedge meadows. Transects across intact sedge meadows

had higher proportions of sedge cover and non-moss vegetation cover, and higher numbers of hummocks and woody stem counts.

Bird abundance comparisons. We estimated abundance for four species and two guilds in freshwater sedge meadows. For all species and guilds, we observed lower abundance in altered areas compared to intact habitat patches (Table 3). Based on GLM analyses for species and guilds, survey timing did not explain differences in bird abundance across transects (all $P > 0.20$), but habitat condition did explain variation in abundances of Savannah Sparrows, Lapland Longspurs, shorebirds, passerines (all $P < 0.02$), and Semipalmated Sandpipers ($P < 0.10$). Habitat condition was not a significant predictor of Dunlin abundance (Table 3).

DISCUSSION

ABUNDANCE TRENDS AT THE STUDY-SITE SCALE

The most abundant breeding birds on our Cape Churchill study area did not decline in density over time at the study-site scale, despite changes in vegetation resulting from goose herbivory. Population densities of shorebirds were variable among species and years and across spatial scales. At the scale of our study area, the relatively common Semipalmated Sandpipers increased in density, contrasting with nearby population declines reported by Jehl (2007). This species can use freshwater habitats along a spectrum of habitat conditions (Sammler 2001). Dunsins exhibited considerable interannual variation with low densities in 1999 relative to 1984 and 2000. We found no evidence of declines in abundance of passerines,

TABLE 3. Vegetation characteristics and bird abundances (mean number of birds km^{-1}) along transects (200 m in width) in altered (evidence of vegetation alteration from goose herbivory) and intact freshwater sedge meadows at Cape Churchill, Manitoba, Canada, June 2000. Comparisons were made for vegetation characteristics using two-tailed t -tests and for bird abundance using general linear models accounting for ordinal date.

Vegetation characteristic	Intact	Altered	t	df	P
	Mean \pm SE	Mean \pm SE			
% bare ground	14 \pm 5	43 \pm 11	–2.6	5	0.03
% moss cover	7 \pm 3	37 \pm 12	2.8	5	0.003
% bare ground and moss cover	28 \pm 4	88 \pm 4	–9.6	5	<0.001
% sedge cover	39 \pm 5	7 \pm 5	4.6	5	0.003
% non-moss vegetation cover	71 \pm 5	12 \pm 4	9.0	5	<0.001
Number of woody stems	2 \pm 0.2	0.2 \pm 0.1	5.5	5	0.001
Number of goose droppings	4 \pm 0.2	8 \pm 2	–2.6	5	0.06
Number of grubbed pieces	0.1 \pm 0.1	4 \pm 2	–1.5	2	0.13
Number of hummocks	5 \pm 1	0.1 \pm 0.1	9.5	3	0.001
Bird species or guild	Mean \pm SE	Mean \pm SE	$F_{1,13}$	P	
Semipalmated Sandpiper	4.3 \pm 0.4	2.2 \pm 0.9	3.5	0.09	
Dunlin	3.9 \pm 0.8	0.8 \pm 0.4	2.0	0.18	
Savannah Sparrow	7.4 \pm 1.3	4.0 \pm 1.7	8.4	0.02	
Lapland Longspur	4.2 \pm 0.4	0.8 \pm 0.4	28.5	<0.001	
Shorebirds	9.7 \pm 0.8	3.0 \pm 0.5	22.7	0.001	
Passerines	12.7 \pm 1.5	5.2 \pm 1.6	37.4	<0.001	

regardless of their primary habitat associations. The dominant plant community across our study area, freshwater sedge meadow, is used by Lapland Longspurs and Savannah Sparrows for breeding and foraging. By 1999–2000, the freshwater sedge meadows in our study area had not been severely altered by goose herbivory, except in localized patches. Because tundra passerines have relatively small area requirements, large-scale and widespread habitat alteration in freshwater sedge meadows may be needed to elicit population density changes. In addition, substantial interannual variation in abundance of passerines limited our ability to assess change in density in our study. Variation in late spring and early summer temperatures did not explain abundance patterns; significant differences in abundances between the two warmer-than-average years (1984 and 1999) were as common as differences between 1984 and the cooler-than-average year (2000).

Herring Gulls increased on our study area from 1984 to 1999–2000. High prey abundance likely influences populations and reproduction of Herring Gulls, which are opportunistic and generalist predators (Pierotti and Good 1994). The increase in Herring Gulls in our study may have resulted from increased prey resources in the form of Lesser Snow Goose goslings. Gulls regularly take eggs and goslings (Walter 1999), which provide easy and large food items to feed themselves and their broods, and likely switch to this food resource when it is abundant. In a large arctic goose breeding colony in northern Canada, Glaucous Gulls (*Larus hyperboreus*) changed their diets to almost entirely goose resources when goose nesting began (Samelius and Alisauskas 1999). Snow Goose gosling densities at our Cape Churchill study site have increased since the late 1980s (DEA, unpubl. data) due to the overland migration of Snow Goose adults with broods from the growing and expanding colony at La Pérouse Bay. Increases in gosling numbers on our study area between 1984 and 1999–2000 have likely provided gulls abundant food and favored high reproductive success and subsequent population increases.

Our data suggest that populations of some large-sized, ground-nesting species, such as Arctic Terns and Willow Ptarmigan, have declined in our study site. Whether the declines are related to changes in tundra habitat conditions, however, is not clear. Many historical tern-nesting areas at Cape Churchill no longer support terns (JES and DEA, unpubl. data). Tern breeding-site fidelity is not well known, although there is some indication of a high degree of site fidelity for some colonies (Bergman 1980). Willow Ptarmigan are year-round residents, so it is likely that observed declines in abundance of this species at Cape Churchill are related either to local conditions or to annual fluctuations in their populations (some Willow Ptarmigan populations cycle). Pectoral Sandpipers breed irregularly along the Hudson Bay coast in northern Manitoba (Manitoba Avian Research Committee 2003); their primary breeding range is substantially north of Cape Churchill. Although male Pectoral Sandpipers displayed

at our Cape Churchill study area in 1983 and 1984 (Moser and Rusch 1988), this species has not occurred regularly during the breeding season since then (DEA, unpubl. data). The dramatic differences in abundance of Pectoral Sandpipers between 1984 and 1999–2000 are probably not related to changes in habitat conditions at Cape Churchill, but rather reflect that they only occasionally breed on our study site.

The primary predators likely to negatively affect nesting success of many birds in our study area are Herring Gulls, Parasitic Jaegers (*Stercorarius parasiticus*), and arctic fox (*Alopex lagopus*). Gulls have increased in our study area and are highly opportunistic, particularly in the beginning of the breeding season. Parasitic Jaegers likely do not have a large effect on breeding bird populations because jaegers defend relatively large territories (Wiley and Lee 1999), and only 3–4 pairs inhabit the study area during a given year. Arctic fox are likely the most important nest predator, and increased fox densities have been linked with decreased Canada Goose nest success at Cape Churchill (Walter 1999, Reiter 2006). Arctic fox are opportunistic and consume bird eggs and adults (Fay and Stephenson 1989, Prestrud 1992, Samelius et al. 2007).

Some species, specifically medium- to large-sized ground-nesting birds such as Pacific Loons, Long-tailed Ducks, Willow Ptarmigan, and Arctic Terns may have declined on our study area because of changes in the predator community in response to Lesser Snow Goose abundance. Until 1990, few Lesser Snow Geese in the region nested outside of the breeding colony centered at La Pérouse Bay (Cooke et al. 1995), and breeding Snow Geese were not abundant on our study area during the breeding season until synchronized hatching occurred in mid- to late June. At hatching, large numbers of geese walked their goslings from the La Pérouse Bay breeding colony to our Cape Churchill study area (a phenomenon that first occurred in the mid- to late 1980s; Cooch et al. 1993, DEA, unpubl. data). Goslings as an abundant food resource, even though not available until the third or fourth week of June, may encourage high predator densities. However, prior to the influx of Snow Goose broods, predators prey on other species and therefore may exert high predation pressure on other birds. Early nesting, medium- to large-sized birds, such as Canada Geese, Willow Ptarmigan, and Arctic Terns may, as a group, be an important source of food for predators during the beginning of the nesting season. With high predation pressure, the likelihood of nest failure increases. Recruitment in the presence of high predation pressure may be below levels needed to maintain stationary populations.

ABUNDANCE TRENDS OF BIRDS IN FRESHWATER SEDGE MEADOW HABITAT

Semipalmated Sandpipers, Dunlins, Savannah Sparrows, Lapland Longspurs, shorebirds, and tundra-nesting passerines occurred more frequently in intact sedge meadow habitats

than similar habitats altered by goose herbivory. We found no evidence, however, that these populations declined over time at the scale of the study area. Across much of our study area, there appear to be adequate amounts of intact and appropriate habitat for many birds. Therefore, the differences in density we observed at the habitat-patch scale may indicate that a threshold in extent and degree of habitat alteration may have to be reached for declines in densities of some species to be exhibited at a larger spatial scale. Our results suggest that even a moderate amount of intact or even slightly to moderately altered sedge-meadow habitat may still provide resources adequate for many bird species, particularly passerines, to persist and increase in abundance.

MANAGEMENT IMPLICATIONS

Concern regarding the effects of high goose abundance on tundra ecosystems has sparked a call to reduce size of some populations of Lesser Snow Geese and Ross's Geese (Batt 1997). Impact on other breeding birds, mitigated through effects on vegetation, has been one of the justifications for reducing goose abundance, although few assessments of these potential effects have been made (Ankney 1996). Clearly, Snow Goose herbivory has dramatically altered salt marsh communities throughout large portions of the North American Arctic and sub-Arctic (Jefferies et al. 2006). However, the majority of the tundra landscape in our study area and elsewhere is comprised of freshwater sedge meadows, and in our study area through 2000, these habitats were relatively intact, despite increasing use by Snow Geese over time and dramatic habitat alteration in localized areas. At our Cape Churchill study area, most bird populations did not decline in density over time at the landscape scale, even as Snow Goose use and habitat alteration had increased. Our results suggest that effects on breeding birds using these habitats were not clearly exhibited at the scale of our study area under conditions present through 2000.

At the habitat-patch scale, effects of goose herbivory on densities of breeding birds in our study were evident, suggesting that if habitat alteration is widespread and severe, population declines may occur, even in the extensive and common freshwater sedge meadows. The Lesser Snow Goose colony at La Pérouse Bay has expanded, and smaller clusters of breeding geese have become established and successfully raised broods in freshwater sedge meadows. Expansion of Lesser Snow Goose breeding colonies and foraging by migrating and staging geese could result in increased herbivory pressure and more rapid alteration of such areas. With current population levels and reproductive potential of Snow Geese, alteration of freshwater sedge meadows could be widespread and of such magnitude to cause declines at a broader scale of bird populations that use this plant community for breeding and foraging. Increasing Snow Goose populations may also influence predator population dynamics, which may in turn negatively

affect medium- to large-bodied early-nesting bird species (see Reiter [2006] for a description of predator-prey-alternative prey dynamics in this landscape).

Our study also poses further implications for data interpretation within emerging large-scale avian monitoring programs. Surveys in our study met the general quantitative goals for comprehensive avian monitoring (80% power to detect a 50% decline in 20 years, using a two-tailed test with a significance level of 0.10; Bart et al. 2004) and for the Program for Regional and International Shorebird Monitoring (PRISM, the same goals but specifying a significance level of 0.15; Bart et al. 2005). The coefficient of variation (CV) required to meet the PRISM standard is 0.31 or lower (J. Bart, U.S. Geological Survey, pers. comm.), and the CVs for most bird-year combinations in our study were < 0.31. However, the interannual variation in population size in our study, as reflected by large differences in densities between 1999 and 2000, was substantial for Dunlins, Lapland Longspurs, and Savannah Sparrows, confounding our ability to draw conclusions about population declines or increases and suggesting that monitoring efforts need to consider potentially wide interannual variation in arctic and sub-arctic systems.

ACKNOWLEDGMENTS

The U.S. Geological Survey Cooperative Fish and Wildlife Research Unit Program, the Minnesota Cooperative Fish and Wildlife Research Unit, and the Wisconsin Cooperative Wildlife Research Unit provided funding for this research project. The Mississippi Flyway Council provided logistical support for this project through the operation of the Nestor One Research Camp at Cape Churchill, with funding and in-kind support for Nestor One provided by the Minnesota Department of Natural Resources, the Iowa Department of Natural Resources, the Missouri Department of Conservation, the Arkansas Game and Fish Commission, Manitoba Conservation, the U.S. Fish and Wildlife Service, and the Canadian Wildlife Service. D.H. Rusch (deceased) provided support for SKS at Nestor One and advice on placement of transects. R. Renkin, C. W. Boal, R. Holbrook, S. Maxson, and B. Pember assisted with data collection, and R. M. Zink, F. J. Cuthbert, C. W. Boal, J. Jehl, K. Abraham, and an anonymous reviewer read previous drafts of this manuscript and offered constructive suggestions for improvement. M. Gillespie and T. Kanikula provided logistical and administrative support that made this project possible.

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